microtubules cooperate with an *indirect* mechanism mediated by an mDia–APC/EB1 association? Alternatively, cells may utilize a direct or an indirect microtubule stabilization mechanism depending on the specific context. For example, one mechanism may be invoked in mitotic cells for microtubule search-and-capture, whereas migrating cells may employ a different mechanism to establish cell polarity. In either case, it will be interesting to reveal how cells might employ the two mechanisms in different scenarios.

Another important question will be to identify whether microtubule binding is unique for mDia2? The FH2 domain primary amino acid sequences of mDia1 and mDia2 are highly conserved [5]. Both mDia family members nucleate and processively elongate actin with similar efficiency and both can stabilize microtubules [9,15]. Despite these similarities, mDia2 has demonstrated subtle biochemical differences from its relative.

Previous work has shown that mDia2 bundles F-actin whereas mDia1 does not [16]. Also, mDia2 activity alone is inhibited by the shared mDia1/mDia2-binding partner Dia-interacting protein (DIP) [17]. This is surprising given that DIP binds to the FH2 domain of both proteins with equal avidity. The structural/biochemical explanation for these differences remains unsolved. Clearly, more mDia1/mDia2 comparison–contrast experiments addressing these topics are needed, as well as experiments using more divergent formin family members.

The observations by Bartolini *et al.* [14] raise the possibility that formins not only act as actin assembly factors but also as microtubule-binding proteins to cross-link the two cytoskeletal components. The mDia formins are now poised to play a central role in uniting the mechanisms controlling both actin and microtubule dynamics. An additional candidate for this role is the microtubule-binding protein APC. In a previous collaborative effort between the Gundersen and Goode labs [18], APC was shown to affect F-actin dynamics through direct binding and bundling of F-actin.

The impact of these studies may also provide insight on the contribution of microtubule stabilization and actin dynamics in diseases such as cancer. mDia1 appears to harbor tumor suppressor activity [18] while defects in the APC tumor suppressor gene drive the progression to malignant colon cancer [19]. It is also interesting to consider that a potent microtubule stabilizing agent – taxol – is commonly used in the clinic to treat cancer. While the mechanism of microtubule stabilization is different between mDia and taxol, the potential exists for mDia-mediated microtubule stabilization to be a promising therapeutic target. Insight into the mechanism of Rho–mDia microtubule stabilization will certainly be an important focus of research in the future.

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Social Learning: Nectar Robbing Spreads Socially in Bumble Bees

Social transmission of learned behaviour is well documented in vertebrates but much less so among invertebrates. New research shows that nectar robbing can spread socially among bumble bees, even in the absence of nectar-robbing models.

David F. Sherry

Bumble bees are robbers. Along with acting as legitimate pollinators — collecting nectar and pollen and transporting pollen between flowers — bumble bees also circumvent floral structures designed to ensure pollination by biting into corolla tubes and floral spurs to obtain nectar. Because of their relatively large size, bumble bees, along with carpenter bees and flower-piercing birds, are the major nectar-robbers that insect-pollinated plants contend with [1]. Bumble bees are also sophisticated learners, capable of learning novel flower-handling techniques [2],

estimating the duration of time intervals [3], and making complex foraging decisions [4]. In a recent report, Leadbeater and Chittka [5] asked whether bumble bees can learn from each other how to rob flowers.

Social transmission of learned behaviour has the potential to produce rapid change in the behaviour of a population of animals [6]. Social transmission can cause a novel behaviour to propagate very quickly compared to change produced by natural selection, and can do so at an accelerating rate as more individuals acquire the novel behaviour [7]. Behaviour acquired by social transmission can also expose animals to selective pressures they would otherwise not be affected by. Socially acquired exploitation of a new food, for example, can cause selection for behavioural and physiological adaptations for processing this new food.

Although it is often assumed that observational learning, imitation, or copying, lies at the heart of social transmission, there are many ways novel behaviour can be transmitted socially without imitation. The presence of conspecifics may draw an animal into a context in which it has the opportunity to learn new behaviour, a process called local, or stimulus, enhancement [8]. Animals that have learned a novel behaviour can also change the environment in a way that makes it easier for naïve animals to learn the behaviour [9], and it is this form of social transmission that Leadbeater and Chittka examined.

Bumble bees that rob flowers by biting a hole in the corolla tube leave behind flowers with a hole near the nectary. This consequence of nectar robbing may make it easier for naïve bees to learn the nectar-robbing technique and result in social transmission of nectar robbing even in the absence of opportunities for observational learning or imitation.

Leadbeater and Chittka [5] exposed naïve bumble bees (*Bombus terrestris*) to broad bean (*Vicia faba*) flowers mounted on syringes through which a small volume of sucrose was continuously pumped to serve as floral nectar. Corollas were either intact, with tape around the tubular base to prevent biting and robbing by bees, or had a 2 mm hole through the tape and corolla permitting bees to take sucrose without entering the corolla tube and their proboscis to reach nectar in the standard fashion. Naïve bees in two groups were exposed to either intact flowers or punctured flowers for 30 minutes and then observed as they foraged on intact untaped flowers. Bees in both groups bit flowers but while bees exposed to intact flowers directed most of their bites to the flower petals, bees exposed to punctured flowers (simulating flowers robbed of nectar by other bees) bit at the base of the corolla tube where they could gain direct access to nectar (Figure 1). Exposure to robbed flowers promoted robbing by directing biting to the right place on the flower.

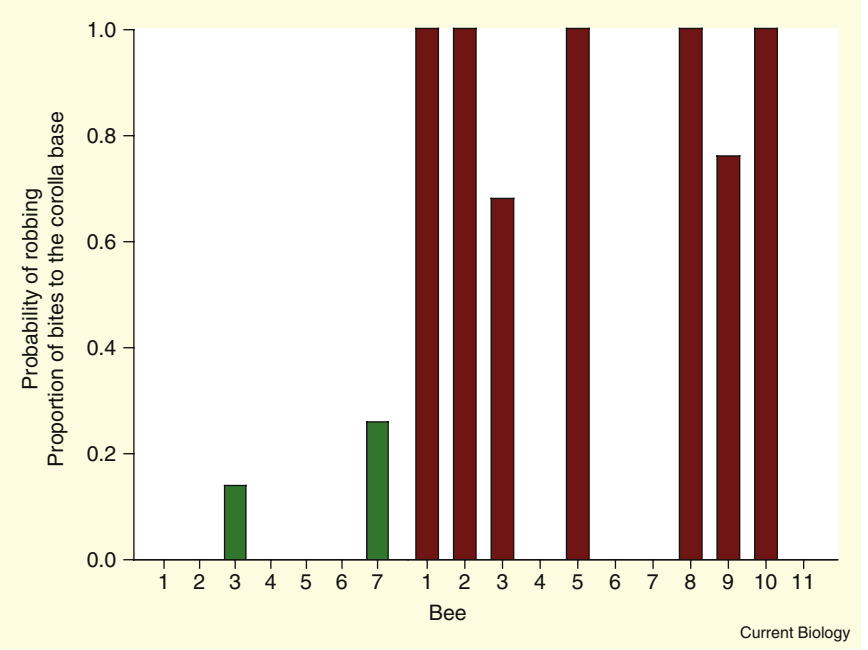

Figure 1. Social learning in bumble bees.

Bumble bees with 30 minutes experience foraging on intact broad bean flowers directed most of their biting at flower petals and relatively little at the corolla base (left) while other bees with 30 minutes experience with flowers that had a 2 mm hole in the corolla base, simulating prior nectar robbing, directed most of their biting to the corolla base (right). (Adapted with permission from [5].)

In a further experiment to test the effectiveness of observational learning of flower robbing, naïve bumble bees were allowed to forage on artificial paper flowers that had a pre-cut hole at the base of the corolla tube. Naïve bees in two groups foraged for 30 minutes, either in the company of bees that had been trained to feed exclusively from the pre-cut nectar robbing hole or in the company of bees that had been trained to feed exclusively in the standard fashion, by entering the corolla tube. Nearly all of the naïve bees probed the pre-cut holes with no difference between the two groups (14 out of 15 naïve bees exposed to robber demonstrators and 13 out of 15 naïve bees exposed to legitimate nectar foragers). The only difference between naïve bees exposed to robbers and those exposed to legitimate foragers was a tendency to probe flowers at a shorter latency. This shorter latency, however, occurred for probes at both the pre-cut hole and at the standard entrance of the corolla tube.

Leadbeater and Chittka [5] attribute this general reduction in latency by naïve bees foraging with nectar robbers to their attraction to flowers where robbers were foraging. Robbers remain visible on the outside of the flower as they probe for nectar while legitimate foragers may be hidden by the corolla and bumble bees are known to be attracted to other foragers on flowers [10]. Nectar robbing is thus socially transmitted highly effectively between bumble bees but not by observational learning. Instead, evidence of the break in at the scene of the robbery makes naïve bees more likely to learn to rob.

The textbook case of social transmission of behaviour in vertebrates is Fisher and Hinde's [11]

account of the spread of milk bottle opening by British tits. Fisher and Hinde collected reports on the spread of milk bottle opening in Britain from the 1920s to the 1940s and concluded that the behaviour was socially transmitted. They were cautious, though, about attributing the spread of milk bottle opening to learning by observation. In black-capped chickadees — closely related North American members of the chickadee and tit family — exposure of naïve birds to milk bottles opened by milk bottle robbers is as effective in promoting milk bottle opening by naïve birds as is observing a demonstration of milk bottle opening by another bird [9]. In both bumble bees and birds, changes to the environment brought about by novel behaviour are as effective a means of social transmission as observational learning and may require less complex cognitive processing on the part of naïve animals.

Social transmission of flower robbing among bumble bees suggests that once the behaviour occurs in a population of bees it can quickly become widespread. What are the consequences of nectar robbing for insect pollinated plants? Remarkably, nectar robbing may not be all bad [1]. Nectar robbers can acquire pollen and transfer it between flowers just like legitimate pollinators. The reduction in available nectar caused by robbing can result in longer flight distances between flowers by legitimate pollinators, promoting outcrossing. Robbing can cause shorter visits by legitimate pollinators and a reduction in pollen transfer, but this may be balanced by fewer visits to flowers within the same inflorescence and also promoting outcrossing.

The potential for social transmission of novel behaviour in pollinators opens many promising avenues of research about the plasticity of invertebrate behaviour, the consequences of sociality, and the complex web of interactions between plants and their pollinators.

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Evolutionary Genetics: Changed Sex Determination in Honeybees

In several insects and fish, and probably some mammals, the gene controling the male–female switch has changed during evolution. It now seems that this has also happened in honeybees, where the sex-determining gene has now been shown to be a duplicate of another Hymenopteran sex-determining gene.

Deborah Charlesworth

Sex-determining pathways seem to be particularly malleable during evolution — the gene that gives the earliest sex-determining signal to the developmental system can change [1,2], while downstream parts of the pathway are retained. This was first noticed when genes involved in the *Drosophila* male–female developmental switch were compared with those in other Dipteran species [1,3,4]. These inferences have been confirmed by recent functional studies [3,5,6]. Changes have also occurred in fish with genetic sex determination. In the medaka, *Oryzia latipes*, sex determination involves a male-specific region on linkage group 1 that only recently gained this function [7]. The *O. latipes* sex-determining gene, *DmrtY*, was duplicated in this species to this region from another chromosome (linkage group 9), which is not the sex chromosome of related *Oryzia* species — their sex-linked markers map among markers on *O. latipes* autosomal linkage groups 10 and 12, and their functional *Dmrt* genes are not linked to sex-linked markers [7,8]. Some mammals have also probably undergone such evolutionary changes [9]. In humans and mice, the gene for the testis determining factor, called *SRY* in humans, is the earliest 'switch' for the pathway, but some rodents seem to have no *SRY*. Now it seems that honeybees and their close relatives have also replaced one sex determining gene by another [10].

Like other Hymenopteran insects, honeybees have a haplo-diploid sex determining system (reviewed in [11]). Females can lay fertilised eggs, which generally develop as females, or unfertilised ones, which develop as haploid males. In honeybees and several other species, the signal to switch the developmental system to male or female involves a sex-determining locus — the '*complementary sex determination*' (*csd*) locus. The *csd* locus is highly polymorphic, with around a dozen different alleles, presumably at intermediate frequencies in populations, so that most diploid zygotes are heterozygous. Haploid zygotes are, of course, never heterozygotes, so that heterozygosity for different alleles can serve as a signal to control the developmental